Evaluation of Philippine *Gemmula*: I. Forms Related to *G. speciosa* and *G. kieneri*

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ABSTRACT

Gemmula (Weinkauff, 1875) is the largest genus in the subfamily Turrinae (H. & A. Adams, 1853). In this article, Philippine forms of *Gemmula* with morphological similarities to *Gemmula speciosa* (Reeve, 1843) and *Gemmula kieneri* (Doumet, 1840) are evaluated. Two new species, *Gemmula sogodensis* and *Gemmula sikatunai*, are described. A group of *Gemmula* specimens collected from the Western Atlantic appear to be a form of *Gemmula sikatunai*. The similarity between Philippine and Atlantic forms suggests that *Gemmula sikatunai* is remarkably stable, long-lived species.

Keywords: Turrinae, *Gemmula*, Relict species

INTRODUCTION

The Turrinae (H. & A. Adams, 1853) are a subfamily of venomous gastropods that belong to the family Turridae (H. & A. Adams, 1853), superfamily Conoidea (Ponder & Warén, 1988). We focus in this article on Philippine forms of the genus *Gemmula* (Weinkauff, 1875), the "gemmate turrids" that are related to *Gemmula speciosa* or *Gemmula kieneri*. Most Philippine forms in the subfamily Turrinae fall into three major genera, *Turris* (Röding, 1798), *Lophiotoma* (Casey, 1904), and *Gemmula*.

The first three papers of this series (Olivera, 1999; Olivera, 2002; Olivera, 2004) presented an overview of Philippine species of *Turris* and *Lophiotoma*. Both *Turris* and *Lophiotoma* are strictly Indo-Pacific, and appear to be of relatively recent geological origin, since these genera do not appear to be represented in the fossil record earlier than the Miocene (Powell, 1964). In contrast, the fossil record for *Gemmula* extends back to the Paleocene (Powell, 1964; Powell, 1966). The biogeography of living forms in each genus also supports this picture: *Gemmula* is found not only within the Indo-Pacific, but in the eastern Pacific and Caribbean provinces as well. Powell remarked in the last comprehensive monograph on the Indo-Pacific Turrinae that the genus *Gemmula* "is the most vigorous member of the Turrinae, and undoubtedly represents the main stem of the subfamily" (Powell, 1964). Both in the past and at present, the genus has had a wider radiation than any other genus in the Turrinae.

Because of the significant amount of material collected between 30 and 600 meters by shell-gathering fishermen in the Philippines in recent years, a substantial series of specimens of *Gemmula* have become available. Several previously undescribed Philippine *Gemmula* can be clearly recognized from this recently collected trove of new Philippine material. In this paper, two new species

are proposed on the basis of differences in shell morphology. Unfortunately, the soft parts of most forms in the Turrinae are not available for analysis, and although it would have been far preferable to have diagnosed these species with an accompanying comparative description of the entire anatomy, we were restricted to using only conchological characters. This is a limitation of this work; in particular, as will be described below, specimens of one of the new species proposed are from two widely separated geographic localities, and a more extensive diagnosis of the anatomy of the whole animals may demonstrate differences between these populations that are too subtle to be discerned from the shells alone.

In the earlier monograph on species of *Turris* in the Philippines, the origins of the species complexes in that genus were the subject of speculation (Olivera, 1999). Our study of the forms of Philippine *Gemmula* discussed in this paper, including an almost identical form from the Caribbean, has provided intriguing insights into the evolution of the Turrinae.

MATERIALS AND METHODS

Specimen collection

Gemmula specimens examined were mostly from the author's collection, collected from various Philippine localities. Specimens more recently obtained were collected primarily by using tangle nets in deep water (80-600 m), by trawling, or by hookah in the localities indicated under each species. The Caribbean material examined was collected by A. Kerstitch in 1997 by dredging in deep water off the island of Barbados. Material collected in the Philippines by the *Muséum National d'Histoire Naturelle*, Paris was examined and has proven to be of exceptional value for establishing the bathymetric distribution of several forms. The author also examined material from the following American museums: National Museum of Natural History, Smithsonian Institution, Washington, DC; the Field Museum of Natural History, Chicago, IL; the American Museum of Natural History, New York, NY; and the Los Angeles County Museum of Natural History, Los Angeles, CA.

Species characterization

The primary diagnostic keys used were the monograph of Powell (Powell, 1964), the book of Springsteen and Leobrera (Springsteen & Leobrera, 1986) and the 1983 article by Kilburn (Kilburn, 1983). Morphological observations were restricted to the shells of each species. However, we have also collected alcohol-preserved material wherever possible in anticipation of a comprehensive molecular analysis of the Turrinae.

The *Gemmula speciosa* group

Overview

Gemmula speciosa (Reeve, 1843) is a well-known species found over much of the Indo-Pacific and the Red Sea. Most Philippine specimens in older collections were obtained from trawlers, particularly those operating around Samar Island (Carigara and Maqueda Bays) and Southwestern Luzon Island (Tayabas Bay), where *G. speciosa* was collected in fair numbers in the late 1950s and 1960s, until trawling methods were changed. *G. speciosa* is a relatively large species (attains >75 mm), with golden brown spiral cords on a white background, a brown cog-like peripheral cord and a rounded body whorl. The continuous golden-brown color of primary spiral cords without interruption is one defining characteristic of typical shells of the species, although substantial variation is observed in the intensity of the brown coloration.

More recently, similar specimens from other Philippine localities have been collected by gill nets; these are noticeably more slender and elongate than the material collected by trawling. The author was given a collection of Turrinae from the Caribbean, personally collected by the late Alex Kerstitch. This collection included forms similar to the more-recently collected material from the Philippines. The rather remarkable biogeographic separation of the Caribbean material, despite its similarity to Philippine material prompted a closer examination of whether there were any consistent differences between the Caribbean material and *G. speciosa* from the Philippines. The conclusion from examining a large number of specimens is that in fact, there are two distinct taxa in the Philippine material

conventionally identified as *G. speciosa*; one of these is practically indistinguishable from the Caribbean specimens.

Classical trawled material agrees with the standard Reeve description of *G. speciosa*. The narrower specimens, apparently all collected from deeper water than true *G. speciosa* are a different taxon, described here as a new species, *Gemmula sikatunai*. Thus, the new species appears to have been found in two widely separated localities, the Philippines and the Caribbean. We also include in this group the recently described *Gemmula lululimi* (Olivera, 1999). The biogeographic range suggests that the present living forms in the *G. speciosa* complex may be derived from a more widely distributed, presumptive ancestral form in the Tethys Sea very similar to *G. sikatunai* that has been largely unchanged for tens-of-millions of years. A detailed description of each form follows, as well as a discussion of differences between the forms. The three species included in the *G. speciosa* complex are shown in Fig. 1.

Gemmula speciosa (Reeve, 1843)

Description (adapted from Powell, 1964).

Adult shell 50-78 mm in height. Fusiform, with tall spire, and long, tapered, and slightly flexed anterior canal. Whorls angulate and carinate at just below middle whorl height; base rather suddenly contracted. Peripheral carina, a square-cut prominent flange densely studded with narrow, laterally compressed and peaked nodules which give a regular cog-like effect. Primary spirals plain, thin but sharply raised, usually three above the carina, one of which is on a moderate subsutural fold, one or two below the carina, and about six on the base exclusive of the canal. The secondary sculpture consists of from one to three plain weak threads in the interspaces of the primaries. The surface is crowded with weak, crisp axial threads. Color pattern of light brown to darker golden brown spirals on a buff background.

The peripheral carina is uniformly colored, and all of the primary spirals are similarly tinted light brown to golden brown. In typical specimens, there are no interrupted markings, dots or dashes. The light amber protoconch is typical of *Gemmula* (Fig. 2), and is followed by nine teleoconch whorls in adult shells. In most specimens, the brown primary spirals become obsolete in the anterior siphonal canal, which becomes pure white.

Collection records

Powell recorded three stations where the depth was noted (27 fathoms and 35 fathoms from two stations in the Philippines, and 73 meters from the Gulf of Oman). More recently, the Musorstrom 3 expedition by MNHN, Paris, collected 18 specimens of *G. speciosa* off Lubang Island, Philippines (11° 45 N, 120° 45 E). The collection station was CD 141, and the depth range was 40-44 meters. The 18 specimens of *G. speciosa* in the dredge haul varied in size from 20 mm to 51 mm; eight of the specimens were dead-collected with large drill holes. The only other Turrinae were three small Gemmulas, including one *Gemmula monilifera*, and two of an unidentified species. *G. speciosa* is apparently collected by divers off Batangas, Luzon Island, Philippines, buried deep in sand (Jose Javier, personal communication).

Gemmula sikatunai, new species

This new species has been generally identified by commercial dealers as *G. speciosa*, but compared to *G. speciosa*, the shells examined are smaller and narrower, and were collected from deeper water. We divide *G. sikatunai* into two forms that have a discontinuous geographic distribution, an Indo-Pacific and a Caribbean form; dead specimens of the latter were collected off Barbados.

Gemmula sikatunai, Philippine form

Description

Adult shell, 40-51 mm in height. Fusiform, with tall spire and a long, relatively broad canal. Whorls strongly angulate and strongly carinate. Peripheral carina is gemmate, with two brown cords at the margins, the more posterior being somewhat stronger. Particularly

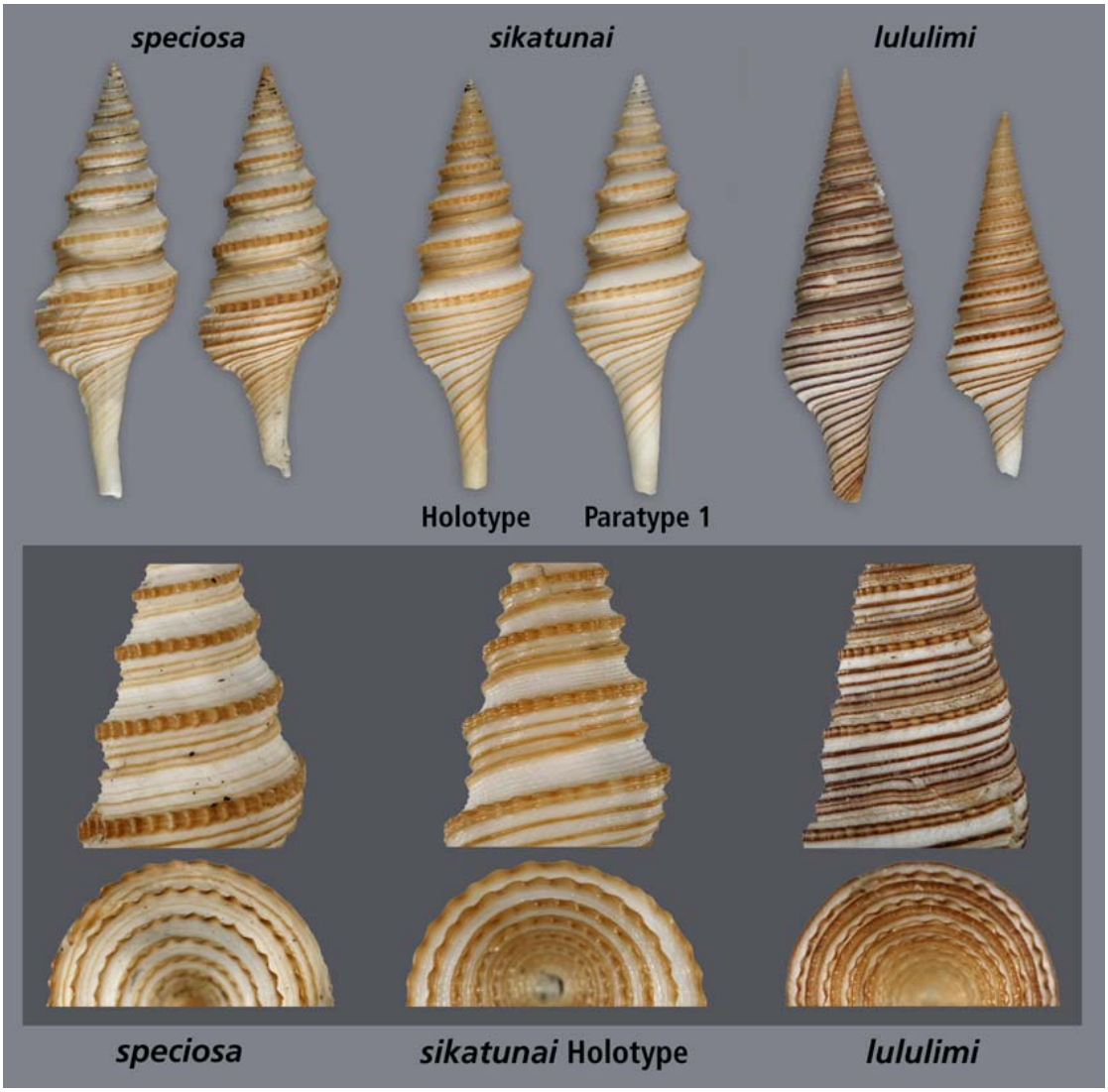

Fig. 1. Top row, from left: *Gemmula speciosa* (leftmost two specimens), *Gemmula sikatunai* (middle two specimens), and *Gemmula lululimi* (rightmost two specimens). For both *G. sikatunai* and *G. lululimi*, the left specimen is the holotype, the right is a paratype. Middle row shows a magnified view to compare subsutural and sinus cord areas. Bottom row: The same specimens showing a top view. Note the continuous brown color and cog-like sinus cord of *G. speciosa*, and the more brown-colored, marginal sinus cord and bead-like structure of the sinus cord in both *G. sikatunai* and *G. lululimi*. Note the lighter central region of these sinus cords in contrast to the uniform brown of *G. speciosa*.

in the larger whorls, the center of the carina and gemmae are lighter colored than the bordering cords; on the body whorl, the two brown cords on the carina are well separated by the lighter-colored central area in mature specimens (Fig. 1). The primary spirals are sharply raised, with one brown primary cord in the subsutural region, somewhat offset from the suture itself. Between the subsutural fold and the peripheral carina are 2-4 white spiral cords. The region between the subsutural fold and the peripheral carina is whiter than the rest of the shell and has a somewhat silky texture. Anterior to the peripheral carina are usually six primary spirals on the body whorl and the base, uniformly light brown to golden brown in color. There are 5-7 additional primary spirals on the canal, becoming progressively lighter and weaker in some specimens, but remaining quite strong almost to the end of the canal in other specimens. The secondary sculpture consists of from 1-3 weak white threads in the interspaces; these become strong towards the base and in the canal, becoming light brown towards

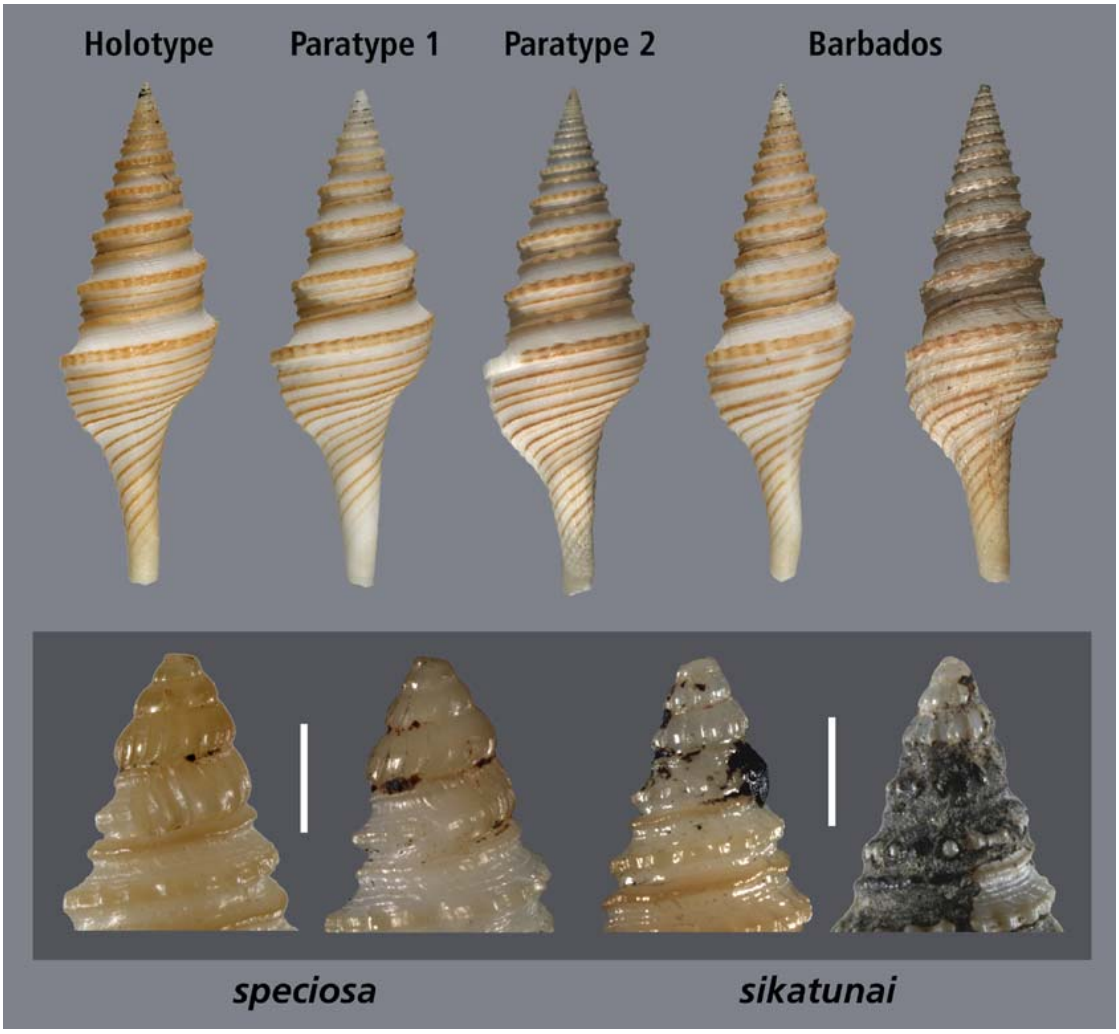

Fig. 2. Top row: *Gemmula sikatunai*, new species. The two rightmost specimens are dead-collected shells off Barbados that are assigned to this species. Bottom row, left two figures: Protoconchs of *Gemmula speciosa* compared to the protoconchs of *G. sikatunai* (these are protoconchs of paratype 13 (left) and the holotype (right)). Note the amber color and larger size of the *G. speciosa* protoconchs compared to the smaller *G. sikatunai*.

the anterior in some specimens. The protoconch is polygyrate with axial ribs, typical of *Gemmula*, and there are ten teleoconch whorls in adult shells.

Nomenclature

This species, found around the Island of Bohol in the Philippines, is named after a 16th century Rajah of Bohol, Sikatuna. In a famous event of Philippine colonial history, Sikatuna and the Spaniard Legaspi entered into a blood compact.

Collection data

The holotype and paratypes 1-5 were collected off Bohol Island, Philippines by gill nets in 100-300 fathoms. The MNHN expedition to Lubang Island, Philippines provides more specific data. The most productive source of *G. sikatunai* was in the Musorstrom 2 expedition, station CP 66, 14° 00 N, 120° E at a depth of 192-209 meters; 42 specimens of *G. sikatunai* were collected in a single dredge haul. Some other stations in the MNHN expedition collections that yielded the new species were station DL 34, Musorstrom 2, 13° 28 N, 120° 12 E at a depth of 155-167 meters (three specimens of *G. sikatunai*) and Musorstrom 1, Station

11, 14° 00 N, 120° 18 E, at 213-230 meters (four specimens of *G. sikatunai*). Seven MNHN specimens are included as paratypes (Appendix). It is notable that in all of the Musorstrom stations at depths >150 m, no specimens of *G. speciosa* were collected. In contrast, in shallower waters (CD station 141, 40-44 meters referred to above) only *G. speciosa* and no *G. sikatunai* were collected. Also included in the paratype series are two specimens in the Los Angeles County Museum (LACM 75849) collected in 52-67 fathoms by J. Norton, near Talaga, Batangas, S.W. Luzon; if these depth records are accurate, it would be the most shallow record for *G. sikatunai*.

Gemmula sikatunai, Caribbean form

This form is strikingly similar to specimens from the Indo-Pacific. However, in addition to the striking geographic separation, there are subtle morphological differences between the two forms.

Description

The adult shell is 39-47 mm in length, with 12-13 whorls. The spire angle is 33-35°, and the siphonal canal is relatively long. All primary spiral cords are uniformly golden brown. On the body whorl, there is a single primary subsutural cord, followed by a white area with six fine white threads. The peripheral carina is made up of two parallel brown spiral cords with gemmules, and on the body whorl there are two pairs of brown primary cords, separated by a white area followed by six to seven less prominent primary spiral threads which cover the base and siphonal canal. The specimens seen by the author are generally more elongate, and somewhat smaller than typical adult specimens of *G. sikatunai* from the Philippines.

Collection data

All known specimens of this subspecies were collected by Alex Kerstitch in June, 1997, in ca. 450 feet off Barbados by dredging. The major turrid collected at this site was a small unidentified *Polystira* species.

Differences between *G. speciosa*, *G. sikatunai*, Philippine form and *G. sikatunai*, Caribbean form

G. speciosa grows to a larger size than *G. sikatunai* (>75 vs. <55 mm for the largest specimens), the whorls of *G. speciosa* are proportionally wider, and the protoconch appears to be larger and smoother. There are a number of consistent differences in sculpture. *G. speciosa* typically has two brown-colored primary cords (range, 1-4) between the subsutural region (which has a primary brown-colored cord in all forms) and the peripheral carina. In *G. sikatunai*, this area is white in all specimens examined. A definitive differentiating feature is the structure of the peripheral carina. In *G. speciosa*, the gemmules are laterally narrow, giving the sinus cord a characteristic "cog-like" structure; furthermore, the entire peripheral carina is generally a uniform brown color, although the intensity of the color can vary markedly. In *G. sikatunai*, particularly in later whorls, the brown color is concentrated on the two edges of the peripheral carina, on raised cords that curve around the gemmules, with a lighter color in between; the gemmules are not narrow and raised, and do not give a cog-like impression.

G. sikatunai is narrower in outline than *G. speciosa*. The whorls of *G. speciosa* are somewhat rounded and contracted at the base; the whorls of *G. sikatunai* are triangular, strongly carinate, with the shoulder area quite sharply angled with respect to the rest of the whorl. Finally, in *G. speciosa*, the brown primary cords tend to become obsolete in the upper half of the siphonal canal, leaving much of the siphonal canal pure white; in many specimens of *G. sikatunai*, the primary brown cords continue almost to the end of the canal.

The Philippine and Caribbean forms of *G. sikatunai* are very similar; all specimens of the latter were dead-collected. In Caribbean specimens, anterior to the peripheral carina are two strong brown primary ribs, followed by a gap with a conspicuous white area lacking a brown cord, followed by more primary cords more or less evenly spaced (in certain specimens, another gap occurs between the cords on the base and the cords on the canal, but this is variable). In Philippine specimens, the brown cords are either more or less regularly spaced, or show an alternating pattern of dark and. light brown primary cords. Caribbean specimens are proportionally

narrower than the typical Philippine form. In Caribbean specimens, the subsutural primary brown cord is more diffuse at the anterior edge. The most intriguing feature of these forms is their remarkable geographic separation.

Gemmula lululimi (Olivera, 1999)

This species has developed a more *Turris*-like shape, but has striking morphological similarities to the *Gemmula speciosa*/*sikatunai* complex in a number of aspects. *G. lululimi* is similar to other forms in the *G. speciosa* group in the continuous golden-brown or blackish-brown color on the spiral cords, on the same whitish background. The number of spiral cords, and the presence of gemmules on the sinus cord are additional characteristics in common.

Description (adapted from Olivera, 1999)

The spire is high, cone-shaped; adult specimens have 15-17 whorls. Spire angle is 25-27°. There are three primary spiral cords, continuous brown colored, in each spire whorl. The subsutural fold has a major primary cord which is raised; in some larger specimens, a second cord is found immediately adjacent to the suture. There is a pronounced depression between the subsutural primary cord and the sinus cord. The sinus cord has gemmules, and in later whorls the two margins are brown, with the central gemmae lighter in color, almost white in some specimens. The sinus cord is not located peripherally, but is posterior to the periphery. A strong brown cord is present at the periphery in all the spire whorls. On the body whorl, there are 5-7 brown primary cords anterior to the sinus cord, with 4-6 brown primary cords on the anterior canal. The very tip of the canal is white, lacking the brown spiral cords in most (but not all) specimens. The specimens the author has examined range in size from 37-87 mm.

Discussion

G. lululimi is unusual among members of this complex in its distinctively different shell morphology, which has some features more consistent with *Turris* rather than *Gemmula*, notably that the sinus cord is not the peripheral carina as in most species of *Gemmula*; in the case of *G. lululimi* the sinus cord is non-peripheral, located instead between the subsutural area and periphery. However, the reasons for including this form in the genus *Gemmula* were discussed with the original description (Olivera, 1999); basically, all other characteristics of the shell have a strong affinity to the *G. speciosa* group, and no apparent phenetic similarity to other species in the genus *Turris*. It should be noted that the structure of the sinus cord, though at a non-peripheral position is more similar to the peripheral cord of *G. sikatunai* than to *G. speciosa* (Fig. 1).

Recently, a number of specimens was collected that are much darker in the color of the primary cords and have a more robust shell than the types. This form has been described as a species within the genus *Turris*, *Turris* (*Annulaturris*) *munizi* by Vera-Peláez et al. (Vera-Peláez et al., 2000), but appears to be conspecific with *G. lululimi*. This species remains relatively rare, and is represented in collections by relatively few specimens.

The *Gemmula kieneri* group

Gemmula kieneri is a widely distributed Indo-Pacific species, and it has become clear that there are two distinct forms in the Philippine material conventionally assigned to *G. kieneri*. A new species, *G. sogodensis* is described.

Gemmula kieneri (Doumet, 1840)

Description (adapted from Powell, 1964)

Adult shell up to 73 mm in height, robust, fusiform, with tall spire and long, rather straight anterior canal. Spire whorls with a strong square-cut keel situated below the middle, not prominently projecting and sculptured, with closed spaced rectangular gemmules that are laterally compressed. There are regular squarish spots between the gemmules. The strong complex subsutural fold is irregularly blotched with brown, and usually consists of a primary cord (sometimes two) and additional threads. Between the subsutural fold and the peripheral keel, there are usually 3-4 sharply raised,

slightly imbricate threads. Between the primary keel and the lower suture there is one primary cord and several threads. One the base, exclusive of the anterior canal, are about 6 primary cords, with irregularly disposed brown spots, with between 1-3 interstitial threads. The surface is covered with dense lamellate axial growth threads that imbricate the secondary spiral threads.

Discussion

Philippine specimens seem to be generally smaller with a proportionately broader spire than specimens from the northern Pacific. The range of variation in Philippine specimens is primarily in the shape of the shell; the ratio of the canal to the spire can vary considerably in Philippine specimens. Specimens from Japanese waters are much more solid, robust shells. This species can normally be differentiated from *G. sogodensis* (see next species) by the irregularly blotched, usually broader subsutural cords, which because they are more prominent and larger, make *G. kieneri* seem much less constricted at the sutures than is the case with *G. sogodensis*. There is also considerable variation in color. In some specimens the whole area from the upper suture to the sinus cord can be quite deeply colored; in other specimens this area is whitish. In a few specimens, the body whorl has axial patches of light brown.

***Gemmula sogodensis*, new species**

A previously unrecognized form, morphologically somewhat intermediate between *G. kieneri* and *G. speciosa*, has been collected in sufficient numbers to convincingly demonstrate that it is distinct from *G. speciosa*, *G. kieneri* and *G. cosmoi* that it can be mistaken for, based on a number of conchological characters.

Description

Adult shells are 36-49 mm in length, with 11-13 whorls in adult specimens. The spire is relatively high, spire angle typically 34-36°. The anterior canal is long, and the ratio of aperture plus canal to total length is approximately 0.5. A single subsutural cord is present of a continuous reddish-brown color, followed anteriorly by a white area with flattened spiral threads. In occasional specimens, one of the threads is light brown in color. The large peripheral, highly gemmate sinus cord is white in the early spire whorls, with the interspaces on the peripheral cord between gemmules becoming brown colored in later whorls. On the body whorl, these interspaces become brown to reddish-brown, with raised white gemmules. The body whorl has about six primary spiral cords in addition to the peripheral sinus cord, each with an irregular pattern of golden or reddish-brown dots and white raised dashes. The cords on the body whorl are much less prominent than the sinus cord. On the sixth spiral cord there is usually a second sinus that forms on the lip. The canal is covered by numerous white spiral cords which are more flattened and less colored than the body whorl cords. The combination of the prominently gemmate sinus cord with white gemmae and golden or reddish-brown interspaces which are white in early spire whorls and become more deeply colored as the shell whorl gets larger, the uniformly colored subsutural cord, and the presence of a second sinus are distinctive characteristics of the species. The holotype and several paratypes are shown in Fig. 3.

Collection data

The type locality for *G. sogodensis* is Sogod, Cebu, Philippines, for which the species is named. Most Philippine specimens known to the author that have been collected recently were from the type locality. The specific collection site is off Barangay, Tabunok, Sogod in the central Philippine island of Cebu. *G. sogodensis* specimens were obtained using tangle nets that are approximately 600 meters long, at a depth of 60-100 fathoms. The specimens were collected from a black mud bottom, with a sand-silt substrate with high organic matter, approximately 1 km offshore from Tabunok. The specimens had a pitch black coating which is removed when the shells are soaked in bleach and brushed off. *Conus* from the same locality including *Conus tribblei* and *Conus pagodus* are typically covered with a green algae, while some *Conus* and turrids (*Conus sulcatus* and *Lophiotoma bisaya*) are collected much more cleanly, with only the periostracum. The origin of the dark coating on the shells of *G. sogodensis*

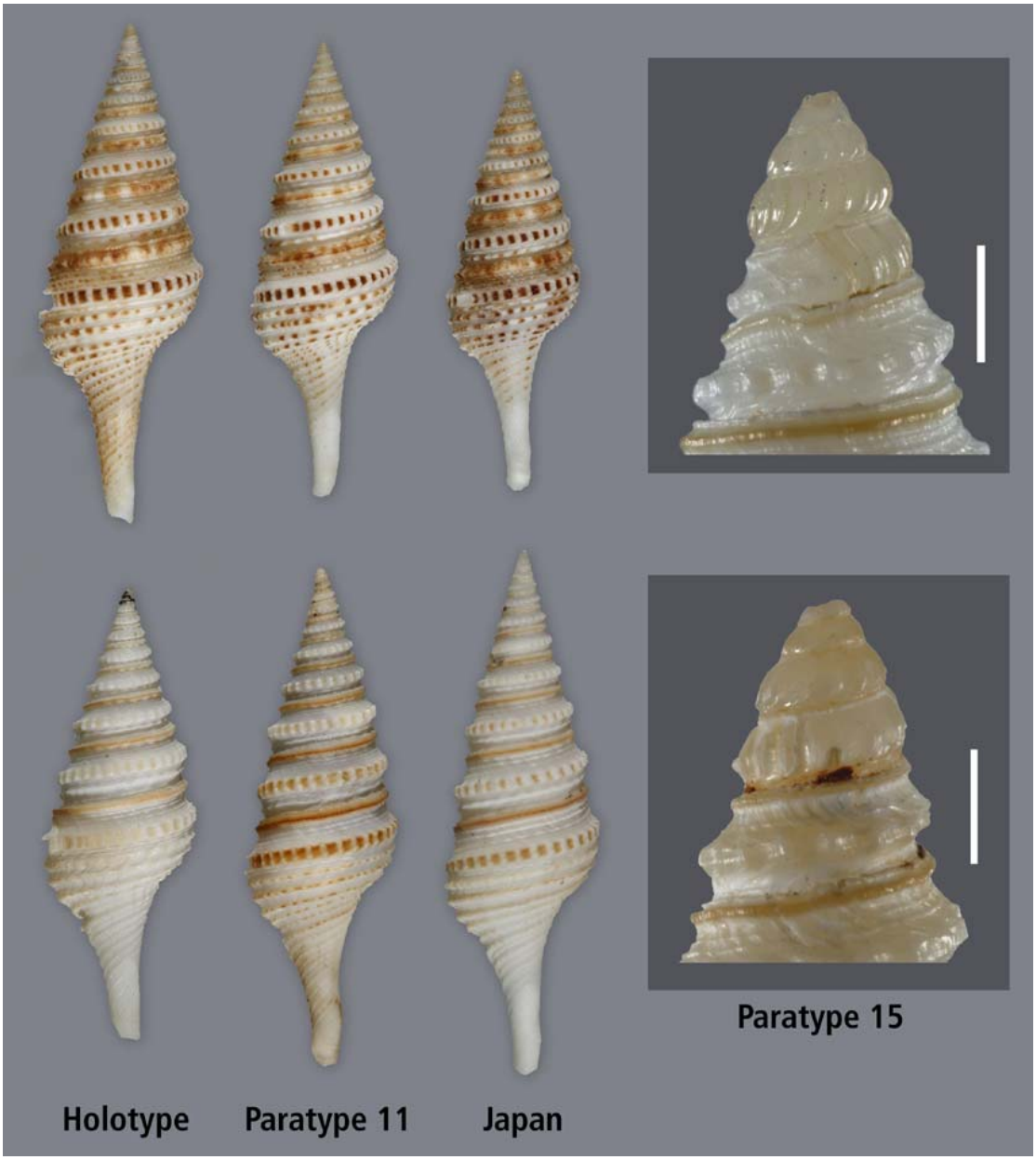

Fig. 3. Top row: Specimens of *Gemmula kieneri* and a protoconch of *G. kieneri* (extreme right). Bottom row, from left to right: *Gemmula sogodensis*, holotype, paratype 11 and a specimen from Southern Japan, as well as the protoconch of paratype 15. The bar is 1 mm.

must have some specific biological determinants. *G. sogodensis* appears to be one of the most common turrids at this locality; the main commercial product of this shell fishery is *Murex troscheli*, a large decorative *Murex* species. The specific information regarding specimen collection at the Sogod, Cebu locality was kindly provided by Frank Heralde.

Specimens of *Gemmula sogodensis* have been collected from N. Mindanao Island in the Philippines to Taiwan and Southern Japan. One immature specimen collected by the MNHN Musorstrom 3 expedition to Lubang Island, Philippines was collected at station CP 86, 14°00N, 120°18E in 187-192 meters.

Discussion and comparison

Superficially, *G. sogodensis* seems intermediate between Philippine forms of *G. speciosa* and *G. kieneri*. The new species is easily differentiated from *G. speciosa* because the gemmae on the peripheral cord are mostly white; in *G. speciosa*, the peripheral carina has a continuous golden-brown color, including the gemmae. The spiral cords in *G. sogodensis* are not continuously colored but interrupted on the body whorl (there are exceptional specimens where the spiral cords are uniformly colored with light brown). In this respect, *G. sogodensis* resembles *G. kieneri*, but it is easily differentiated from that species by the continuous brown color of the primary cord in the subsutural area and the white peripheral carina in early spire whorls. In *G. kieneri*, the subsutural cord is usually broad, with a complex structure, and irregularly maculated. The brown or reddish-brown subsutural cord of *G. sogodensis* is sharp, crisp and continuously colored (in this respect, more similar to *G. speciosa*). Philippine specimens of *G. kieneri* generally have a higher frequency of gemmules, and on the spire whorls the alternating light and dark color intervals are maintained even on the early spire cords. Other differences are the generally narrower, more elongate spire of *G. sogodensis* compared to *G. kieneri*. Although many specimens of *G. sogodensis* have shells with growth scars, and are often corroded, the best specimens are among the most elegant and attractive of all *Gemmula*.

G. sogodensis may also be confused with *Gemmula cosmoi*, but the former has both brown color in the interspaces between the gemmules and the sinus cord, as well as dashed brown markings between white areas on the primary cords of the body whorl; both features are generally lacking in *G. cosmoi*. In addition, *G. cosmoi* is generally narrower in outline than *G. sogodensis*, and the spiral cords between the brown subsutural cord and the peripheral carina, although white in both species, are much stronger in *G. sogodensis*. Finally, *G. cosmoi* has characteristic comma-like gemmae (Powell, 1964), which are not found in *G. sogodensis*.

Nomenclature

This species name is derived from the type locality, Sogod, Cebu, Philippines.

Types

The holotype will be deposited in the Philippine National Museum. Paratypes will be deposited at the Field Museum of Natural History, Chicago; the National Museum of Natural History, Washington, DC; the Academy of Natural Sciences, Philadelphia; and the American Museum of Natural History, New York City. The paratype series includes two lots from the LA County Museum of Natural History from Taiwan (LACM 69006) and Japan (LACM 47060), and one specimen from the Muséum National d'Histoire Naturelle, Paris (paratype 46).

Distribution of species

It seems likely that *G. sogodensis* will be found to be more widely distributed in the Indo-Pacific. The specimens collected from Taiwan and Southern Japan are documented in the Appendix; the Japanese material has been confused with *G. cosmoi*.

DISCUSSION

A comparison between the *Gemmula* species complex described above and the *Turris babylonia* clade (Olivera, 1999), the dominant group of species in the genus *Turris*, is most instructive. These two groups of species in the Turrinae show striking contrasts: as described above, both the biogeography of *Gemmula* and the fossil record are consistent with an early Tertiary origin for this group, and remarkable stability in *G. sikatunai*. In contrast, both the biogeography and fossil evidence are consistent with a late Tertiary origin for the *T. babylonia* clade of *Turris*. The general impression is that the latter is a relatively young, rapidly evolving species complex.

The data suggest (but do not prove) that *G. sikatunai*, one of the new *Gemmula* species described in this study,

may be an exceptionally stable form. The distinct *Gemmula* species complex found in Philippine waters which is described above has no corresponding living forms in the eastern Atlantic or the Mediterranean. This makes the near identity in conchological characters of the dead-collected Caribbean specimens of *G. sikatunai* to its Indo-Pacific counterpart most striking, given the immense geographic separation, and because the Caribbean tropical marine fauna has long been separated from tropical Indo-Pacific species (since the closure of the Tethys Sea).

It is possible that there has been incomplete sampling of *Gemmula* spp., particularly given that they live in relatively deep water. It is noteworthy that *G. speciosa* has been found in the Red Sea; do these now occur in the Eastern Atlantic, or did they in the past? However, the most straightforward explanation for the biogeography of *G. sikatunai* is that it is of early Tertiary origin, and was widely distributed in the Tethys. This hypothesis needs to be critically evaluated both from additional collection from the eastern Atlantic and eastern Pacific, and by an examination of fossil material.

A priori, it would seem unlikely that in a highly evolved group such as the Turrinae, there might be relict species that are essentially unchanged since the Tethys Sea closed. Perhaps the species evolved after the Tethys Sea closed, since there were migrations east and west of Europe after the late Eocene. Each of these explanations makes specific experimental predictions. The DNA sequence divergence in the two forms of *G. sikatunai* should be subject to analysis by molecular methods; the composition of their venoms, and whether or not there are striking similarities should provide additional data consistent with one of these alternatives. Thus, a comparison of living material should be of exceptional interest. However, given that all Caribbean specimens were dead-collected, the possibility remains that this population is now extinct.

In this report, we have included in the *Gemmula speciosa* group the recently described species *Gemmula lululimi*. Other workers have described the same form, but instead included it in the genus *Annulaturris*, because the sinus cord is not at a peripheral location, a character generally used to diagnose members of *Turris* and *Annulaturris* (the latter sometimes regarded as a subgenus of the former). Given the very striking similarities to *Gemmula sikatunai*, as is documented above, we believe it unlikely that these striking similarities arise from convergence. Furthermore, the species has no phenetic affinities with other species of the genus *Turris* or *Annulaturris*.

We previously hypothesized that *Turris* probably evolved from a *Lophiotoma*-like ancestor (*Lophiotoma bisaya* (Olivera, 2004) was suggested to be one possibility). This transformation of the sinus cord from a peripheral position to one more posterior in each whorl was termed the G-T (*Gemmula-Turris*) transformation. The assignment of *Gemmula lululimi* to the *Gemmula* species group therefore has an underlying evolutionary implication: that this G-T transformation did not occur only once. We suggest that this morphological transformation has occurred at least twice, once to a *Gemmula kieneri*-like descendant that had lost most of its gemmules (to yield *Turris babylonia* and relations) and in a separate event, to a *Gemmula sikatunai*-like form (to yield *Gemmula lululimi*).

The hypothetical conceptual framework is that the Tethys Sea contained ancestral forms of *Gemmula* very similar to *Gemmula speciosa*/*sikatunai* and *Gemmula kieneri*. The latter species complex included forms in which the gemmules were lost (*Unedogemmula*- and *Lophiotoma*-like forms), one of which had a G-T transformation event that was ancestral to most of the modern species in the genus *Turris*. In the case of *Gemmula lululimi* however, the G-T transformation event took place in a *G. sikatunai*-like form that had not lost its gemmules when the G-T transformation occurred. Although this hypothesis is a conjecture at this point, a more thorough characterization of *G. lululimi* should either be consistent with this explanation, or alternatively, should support a closer affinity with other species in *Turris*/*Annulaturris*.

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APPENDIX (prepared by Nancy Kurtzeborn)

Gemmula Species. Measurements and locality data for holotypes and paratypes.

Species	Measurement (mm)			Locality
	Height	Width[a]	Aperture[b]	
Gemmula sikatunai, new species				
Holotype	41.9	13.4	22.0	Bohol Island, Philippines
Paratype #1	45.5	15.4	25.2	Bohol Island, Philippines
Paratype #2	52.0	17.2	26.6	Bohol Island, Philippines
Paratype #3	50.9	15.2	27.2	Panglao Island, Philippines
Paratype #4	41.4	13.8	21.9	Bohol Island, Philippines
Paratype #5	37.1	12.7	20.2	Bohol Island, Philippines
Paratype #6	46.3	14.9	24.9	Bohol Island, Philippines
Paratype #7	59.9	16.1	25.5	Manila Bay, Philippines
Paratype #8	39.2	13.2	20.9	Tayabas Bay, Philippines
Paratype #9	38.6	12.8	21.5	Lubang Island, Philippines (MNHN)[1]
Paratype #10	41.9	13.6	22.1	Lubang Island, Philippines (MNHN)[1]
Paratype #11	39.4	13.7	19.9	Lubang Island, Philippines (MNHN)[1]
Paratype #12	35.0	11.7	19.4	Lubang Island, Philippines (MNHN)[1]
Paratype #13	33.7	11.5	18.5	Lubang Island, Philippines (MNHN)[1]
Paratype #14	33.7	11.3	18.3	Lubang Island, Philippines (MNHN)[1]
Paratype #15	26.2	9.5	14.5	Lubang Island, Philippines (MNHN)[1]
Paratype #16	46.8	14.4	25.4	Luzon Island, Philippines (LACM #75849)[2]
Paratype #17	33.7	10.7	18.5	Luzon Island, Philippines (LACM #75849)[2]
Gemmula sikatunai, Barbados variety				
Specimen #1	41.0	13.4	22.5	Barbados, West Indies[3]
Specimen #2	39.4	12.6	21.2	Barbados, West Indies[3]
Specimen #3	45.8	14.0	23.9	Barbados, West Indies[3]
Specimen #4	42.8	13.4	22.6	Barbados, West Indies[3]
Specimen #5	32.0	10.3	17.3	Barbados, West Indies[3]
Specimen #6	14.7	5.7	7.4	Barbados, West Indies[3] (juvenile)
Gemmula sogodensis, new species				
Holotype	44.5	15.4	23.5	Sogod, Cebu, Philippines
Paratype #1	44.6	15.0	24.3	Sogod, Cebu, Philippines
Paratype #2	40.7	14.4	22.5	Sogod, Cebu, Philippines
Paratype #3	38.4	14.1	21.0	Sogod, Cebu, Philippines
Paratype #4	44.0	14.0	24.2	Sogod, Cebu, Philippines
Paratype #5	46.9	15.3	24.8	Sogod, Cebu, Philippines
Paratype #6	34.6	12.8	20.0	Sogod, Cebu, Philippines
Paratype #7	44.5	16.3	25.7	Sogod, Cebu, Philippines
Paratype #8	43.2	14.2	22.6	Sogod, Cebu, Philippines
Paratype #9	45.6	17.1	24.2	Sogod, Cebu, Philippines
Paratype #10	40.6	16.0	21.0	Sogod, Cebu, Philippines
Paratype #11	48.6	15.3	24.7	Dipolog, Philippines
Paratype #12	50.8	16.6	27.2	Dipolog, Philippines
Paratype #13	45.5	17.3	24.5	Bohol, Philippines
Paratype #14	45.0	15.2	24.2	Bohol, Philippines
Paratype #15	47.4	15.7	23.7	Sogod, Philippines
Paratype #16	46.9	17.6	25.0	Sogod, Philippines
Paratype #17	47.1	15.9	27.0	Dipolog, Philippines
Paratype #18	43.8	14.4	24.3	Dipolog, Philippines
Paratype #19	40.7	15.0	22.2	Dipolog, Philippines
Paratype #20	44.1	15.8	25.7	Dipolog, Philippines

Species	Measurement (mm)			Locality
	Height	Width[a]	Aperture[b]	
Paratype #21	41.1	13.3	23.2	Dipolog, Philippines
Paratype #22	39.1	12.5	20.5	Dipolog, Philippines
Paratype #23	43.2	14.5	23.6	Bohol, Philippines
Paratype #24	30.3	11.4	15.7	Bohol, Philippines (juvenile)
Paratype #25	46.2	16.0	23.6	SW Taiwan (LACM 69006)[4]
Paratype #26	45.4	15.0	24.1	SW Taiwan (LACM 69006)[4]
Paratype #27	57.0	17.4	29.7	Kii, Japan (LACM 47060)[5]
Paratype #28	56.5	18.2	26.8	Kii, Japan (LACM 47060)[5]
Paratype #29	53.8	17.8	28.5	Kii, Japan (LACM 47060)[5]
Paratype #30	54.9	18.7	27.6	Sagami Bay, Japan (AMNH 16519)[6]
Paratype #31	47.4	16.7	26.9	Sogod, Cebu, Philippines
Paratype #32	51.1	17.5	29.3	Sogod, Cebu, Philippines
Paratype #33	50.3	17.9	27.2	Japan
Paratype #34	36.2	13.8	18.1	Bohol, Philippines
Paratype #35	48.0	15.9	26.4	Philippines
Paratype #36	43.5	16.0	21.9	Philippines
Paratype #37	48.4	16.0	25.8	Philippines
Paratype #38	44.5	15.3	23.5	Philippines
Paratype #39	46.9	15.5	25.4	Philippines
Paratype #40	48.6	16.9	17.8	Philippines
Paratype #41	47.2	16.7	25.5	Philippines
Paratype #42	48.6	15.6	26.5	Philippines
Paratype #43	44.6	15.5	25.7	Philippines
Paratype #44	44.2	15.5	24.4	Philippines
Paratype #45	41.5	14.7	21.6	Philippines
Paratype #46	30.0	11.1	16.5	Philippines[7]

[a]Width of shell at its widest point.
[b]Length from posterior of aperture to anterior tip of siphonal canal.
[1]Lubang Island, Philippines; Musorstrom 2-Philippines St. CP66, 192-209 m 14°00N, 120°20E; MNHN-Paris-Malacologie.
[2]East of Talaga, Batangas Bay, Batangas Province, SW Luzon Island, Philippines; 52-67 fathoms on sand and mud bottom, 7/26/66; Los Angeles County Museum of Natural History.
[3]Off Barbados, West Indies; dredged 450 feet, Alex Kerstitch, 6/97.
[4]Tap'ing Ting Chaio, SW Taiwan; trawled, 50-100 fathoms, Leg Franz Steiner, 8/68, ex Thelma Crow; Los Angeles County Museum of Natural History.
[5]Kii, Japan, Birch collection; Los Angeles County Museum of Natural History.
[6]Sagami Bay, Japan, divers 1952; American Museum of Natural History.
[7]Off Lubang Island, Philippines; N.O. "Coriolis" Musorstrom 3, St. CP86 187-192 m, 14°00N, 120°18E, Bouchet & Triclot coll, 31MAI85; MNHN-Paris-Malacologie.